7 The transition between boreal forest and tundra

Luc Sirois

Introduction

The boreal forest and the Arctic tundra are two major biomes which cover a total of 30 million square kilometers in the Northern hemisphere. They are characterized by contrasting dominant life forms and productivity levels associated with the presence of trees in the boreal forest and their general absence in the Arctic tundra. The same general differences exist between forest and grassland but the ecological factors responsible for the position of the forest–grassland transition zone are likely to differ from those operating for the boreal forest–tundra transition zone. A causal explanation of the climate–vegetation pattern of the northern forest border is as yet obscured by the poorly known ecophysiology of the tree species (Oechel & Lawrence 1985). Despite the lack of knowledge of the exact mechanism involved, there is general agreement that thermal characteristics of the climate are of major importance in determining the northern edge of the boreal forest. Somewhere at the interface between boreal forest and tundra, tree species face severe climatic conditions, which reduce their growth and development. This induces changes at the plant population and community levels, which can be observed in the transition zone between these two biomes. Forests of this boundary area are likely to be sensitive to environmental changes and often display low regenerative capacity. Various types of ecological alteration, for example climatic changes and wildfires, take place over a wide range of areal dimensions and in different periods. These result in a temporal and spatial vegetation patterning typical of the northern forest border.

An ecological synthesis of the circumpolar boreal forest–tundra transition zone has not yet been produced. The diversity of tree species, the limited knowledge of vegetation history and of the ecological processes taking place over this large area, as well as linguistic barriers with Russian

literature, make it difficult to attempt a unified treatment of this transition zone as a whole. This chapter will first show the specific differences in and structural similarities of different areas of the circumpolar boreal forest–tundra transition zone. This is achieved by a description of the tree species composition and by a first approximation of a map of the circumhemisperic transition zone. Secondly, it will illustrate what is believed to be climatically induced spatial pattern and temporal dynamics observed in the northern forest borders of a limited number of regions, namely North America, Fennoscandia and the Soviet Union. Finally, the potential role of the fire–climate interaction in the Holocene development of the forest–tundra transition zone is exemplified by a case from north-eastern North America.

Terminology

The great diversity of approaches and criteria which have been used for the characterization and the subdivision of the boreal forest–tundra transition zone has resulted in a non-unified terminology (Ahti, Hämet-Ahti & Jalas 1968; Hustich 1979; Tuhkanen 1984). Frequently used are floristic (Aleksandrova 1980; Andreev & Aleksandrova 1981), climatic (Tuhkanen 1980, 1984) and physiognomic–structural (Hustich 1966; Atkinson 1981; Payette 1983) criteria. These criteria are not reciprocally exclusive and the predominance of one or another is conducive to specific constraints and advantages. The approach chosen depends on the scope and on questions to be investigated. In this chapter, I will use predominantly physiognomic–structural criteria to define zones and patterns. Floristic criteria will be used to illustrate regional specificity, and climatic criteria will be integrated as part of the causative factors. So far, a worldwide-accepted terminology to designate zones and pattern is still lacking (Hustich 1979). Herein, the following terminology and definitions, largely inspired from Hustich (1966, 1979) and Payette (1983), will be used (Fig. 7.1).

Continuous forest limit: Up to this line, forest covers all the water-free landscape features, including upland and lowland (Payette 1983). This limit is believed to be coincident with the isopleth where climate allows sexual regeneration of trees on an annual basis (Hustich 1966). This is a major phytogeographical concept, which still needs to be warranted by time-series data.

Physiognomic forest limit: This corresponds to the limit where forest stands are widespread in mesic sites, regardless of their sexual reproductive capacity (Hustich 1966, 1979).

Forest limit: This is the northern limit of forest stands found in sheltered areas of the northern part of the forest–tundra (Payette 1983).

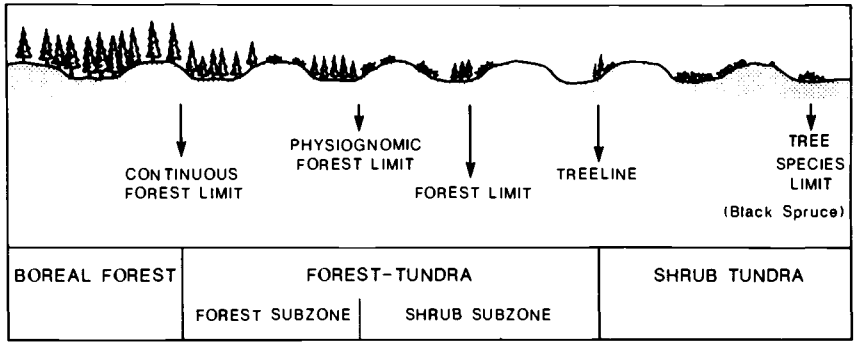

Fig. 7.1. Schematic representation of the major divisions of the boreal forest-tundra transition zone (Payette 1983; redrawn with the permission of the author.)

While the minimum dimensions of these stands have never been stated, they should correspond to a visible entity on a regular (approximate scale 1:50 000) aerial photograph. In this respect, most ecologists do not consider the northernmost so-called 'forests' consisting of Salicaceae species (Maycock & Matthews 1966; Aleksandrova 1980) as constituting the forest limit.

Treeline: This is the northern limit where forest species with an arborescent habit and reaching a minimum height of 5 m (Payette 1983) are found. This concept is totally different from Atkinson's treeline (Atkinson 1981) used in some works (Scott, Hansell & Fayle 1987), which actually corresponds to the continuous forest limit. It differs also from the treeline defined by Larsen (1965) as the zone where forest stands occupy 50% of the soil surface.

The above limits bound the major vegetation zones of the boreal forest–tundra transition zone as follows:

Taiga: Northern part of the boreal forest ranging from the northern limit of the closed crown coniferous forest to the southern limit of the forest–tundra. The northern limit of this zone corresponds to the economic forest-line *sensu* Hustich (1966, 1979), and to the continuous forest limit according to Payette (1983). In the taiga, the mesic forest stands are variously dense, but generally the open-crown lichen woodlands form a continuous cover on the uplands while feathermoss forests or forested bogs occupy the moister lowlands.

Forest–tundra: Vegetation zone lying between the continuous forest limit and the treeline. It is characterized by the patchiness of the forest cover in the landscape, the treeless areas being dominated by lichen and shrub species. The physiognomic forest limit divides the forest–tundra into the forest subzone in the south and the shrub subzone in the north

(Payette 1983) (Fig. 7.1). In the forest subzone the forest cover is widespread in the lowlands but quite sparse on drier upland sites. In the shrub subzone, where the climate has an obvious stressful effect on tree development, the forest stands generally become restricted to a few sheltered sites. Stunted growth forms are a common feature in such an environment; coniferous stands are mostly represented as krummholz.

Regional characterization of the boreal forest–tundra transition zone

The circumhemispheric belt between the southern limit of the taiga and the treeline shows a latitudinal vegetation zonation which is similar in many regions. In contrast, there is longitudinal variation in tree species composition and vegetation pattern; this variation should be considered to gain a global perception of the whole system.

Soviet Union

From Fennoscandia eastward to the Ural range, there is an increasing frequency of *Abies sibirica*, *Larix sibirica* and *Picea obovata* growing with *Pinus sylvestris* in the boreal forest–tundra transition zone. In the more continental climate east of the Ural range, *Larix sibirica* seems to be the most important tree species in the northern part of the transition zone while *Pinus sibirica* is more frequent further south. As the continentality of the climate increases toward eastern Siberia, *Larix dahurica* and *Pinus pumila* are frequent on upland sites (Tikhomirov 1971). These two species form the northernmost forests of the world, reaching lat. 72°N (Woodward 1987). In eastern Siberia, *Populus suaveolens*, *Chosenia macrolepis* and some *Betula* species occur in the valleys (Tikhomirov 1971) and go beyond the coniferous treeline, into the Arctic zone (Aleksandrova 1980). As in north-western North America, the range of most species drops southward near Soviet Beringia (Hustich 1966).

A number of vegetation maps of the Soviet Union (Lavrenko & Sochava 1954; Anonymous 1964) have been translated (Shabad 1965) or reproduced in English reports (Tikhomirov 1960; Hustich 1966; Bazilevich, Drozdov & Rodin 1971; Tuhkanen 1984). It appears that what is defined as the northern taiga zone by Soviet ecologists consists of a continuous, low-productivity forest frequently dominated by *Larix* and *Pinus*. Open-crown forests are a common feature in this area, which extends broadly from lat. 65° to 70°N (Fig. 7.2). It is structurally close to what we consider here as taiga. North of this zone is a strip of forest–tundra dominated by larches and pines and showing a typical patchy distribution of forest stands (Tikhomirov 1971), similar to that observed in the North American forest–tundra.

Fennoscandia

The most frequent tree species in the boreal forest–tundra transition zone of Fennoscandia are *Picea abies*, *Pinus sylvestris*, *Betula pubescens* and *Populus tremula* (Tuhkanen 1980). The deciduous species frequently

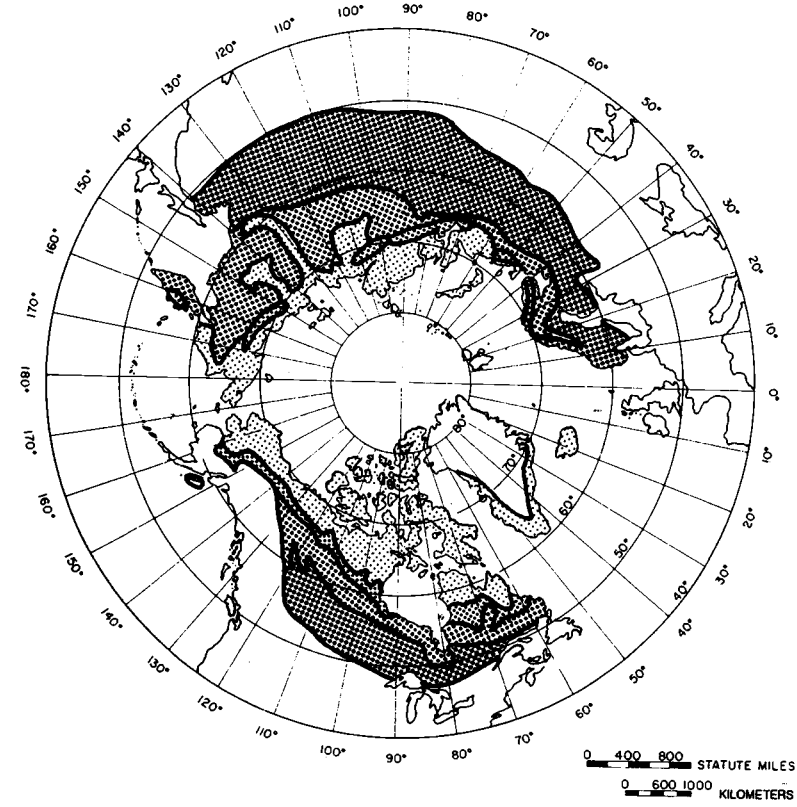

Fig. 7.2. Sketch map of the boreal forest-tundra continental vegetation zones. This map has been produced from information contained in maps from Anonymous (1964), Hustich (1966), Ahti, Hämet-Ahti & Jalas (1968), Krebs & Barry (1970), Tikhomirov (1971), Rowe (1972), Tukhanen (1980), Hämet-Ahti (1981), Olson, Watts & Allison (1983), Payette (1983) and Ritchie (1984).

extend north beyond the coniferous species, presumably in response to the damp oceanic climate (Hämet-Ahti 1963; Sjörs 1963; Ahti, Hämet-Ahti & Jalas 1968; Hämet-Ahti & Ahti 1969). The presence of south–north oriented highlands in Norway, along with a steep west–east oceanity gradient along the Atlantic coast, has a strong influence on the vegetational zonation of Fennoscandia. This is reflected in the maps of Sjörs (1963) and Ahti, Hämet-Ahti & Jalas (1968), both of which show an obvious longitudinal component in zonation. The northern boreal zone of Ahti, Hämet-Ahti & Jalas (1968) corresponds to the subarctic and boreomontane subzones in Sjörs' system (Sjörs 1963). This zone extends from the northern part of Fennoscandia southward into the highlands and seems to be structurally equivalent to what we have defined as taiga. The tree species component of the Fennoscandian lichen woodlands includes mainly *Pinus sylvestris* and to a lesser extent *Betula pubescens* (Oksanen & Ahti 1982). The orohemiarctic zone of Ahti, Hämet-Ahti & Jalas (1968) is named the Woodland–Tundra zone by Sjörs (1963). This zone, a narrow fringe between the northern boreal zone and the maritime tundra in the northernmost part of Fennoscandia (Fig. 7.2), consists basically of forest–tundra where *Betula pubescens* forms the treeline.

North America

In the North American boreal forest–tundra transition zone, the most frequent coniferous species are black spruce (*Picea mariana*), white spruce (*Picea glauca*) and larch (*Larix laricina*). West of Hudson Bay, black spruce and larch are most frequent in poorly drained sites while white spruce dominates in mesic sites. On the Quebec–Labrador peninsula and in Newfoundland, white spruce is restricted to areas influenced by the damp maritime climate of Hudson Bay and the Atlantic Ocean. Inland, black spruce forms almost monospecific forests in a large range of ecological conditions; larch is generally only a secondary species in such forests.

Jack pine (*Pinus banksiana*), fir (*Abies balsamea*) and sitka spruce (*Picea sitchensis*) are less widely distributed species in the transition zone. Jack pine is found in xeric habitats such as sand dunes (Desponts 1990) whereas fir is mainly observed in areas with a maritime–oceanic climate such as Labrador–Newfoundland (Lamb 1985). Sitka spruce is distributed on the Pacific shore, where it forms the treeline on the Alaska peninsula (Viereck 1979). Some deciduous tree species (*Populus balsamifera*, *P. tremuloides* and *Betula papyrifera*) form small populations, frequently associated with ecological disturbances such as fire or flooding, throughout the area.

Rowe's forest map of Canada (Rowe 1972), along with more regional studies (Rousseau 1952; Ritchie 1959; Viereck 1979; Payette 1983),

allows us to depict the general zonation of northern North American vegetation. In Alaska, the treeline is situated at the southern Brook Range piedmont and drops southward from Kotzebue to Kodiak Island (Larsen 1989). The great difficulty in defining latitudinal zonation in this area is attributed to high elevation terrain situated where the forest–tundra transition zone would otherwise exist (Viereck 1979). The relatively flat topography of northern Canada is conducive to a simpler latitudinal zonation. Broadly speaking, the treeline is NW–SE oriented across Canada. It reaches its northernmost position in the Mackenzie River Delta area (lat. 68°N) (Black & Bliss 1978), drops south to James Bay (lat. 55°N) (Rowe 1972) and crosses the Quebec–Labrador peninsula at approximately 58°N (Rousseau 1952; Payette 1983). The area between the treeline and the continuous forest limit, the forest–tundra itself, increases in width from western to eastern continental Canada. This pattern can be partly explained by a southward rise in altitude from Ungava Bay to a point about 150 km north of the St Lawrence River (Hare & Ritchie 1972). Greater fluctuations in the July position of the Arctic air mass in eastern Canada (Bryson 1966) can also increase the width of the forest–tundra in this part of the country. South of the continuous forest limit is the large expanse of open crown forest of the taiga. The ground vegetation in the taiga west of Hudson Bay is generally dominated by shrubs and herbs, although some lichen woodlands are observed on upland sites (Rowe 1972). Lichen woodlands are far less extensive over this area than east of Hudson Bay (Rowe 1984), where they constitute the dominant forest type in the taiga and forest–tundra uplands (Larsen 1989).

Climate–vegetation relations

Elucidation of the relation between the northern vegetation boundaries, especially the treeline, and climatic indices has been a challenge to ecologists for decades. An ambitious attempt to relate climatic characteristics to northern phytogeographical regions is offered by Tuhkanen (1980, 1984). He suggests a system of climatic–phytogeographic regions based on a cubic model in which the axes are gradients of temperature sums, continentality–oceanity and aridity–humidity. The continentality–oceanity gradient, calculated by using the Conrad index, and the aridity–humidity gradient are related to the total precipitation during the growing season. They are not completely independent climatic indicators and appear to be associated mainly with the longitudinal pattern. Tuhkanen (1980) himself agrees that thermal characteristics of the climate, especially during the growing season, are responsible for or at least coincident with phytogeographical boundaries in northern latitudes.

Table 7.1. *Forest divisions and potential evapotranspiration on the Labrador–Ungava peninsula*

Division	Typical value of PE along boundaries (cm)	Dominant cover type
Tundra		Tundra
	30–32	
Forest–tundra		Tundra and lichen woodland intermingled
	36–37	
Open boreal woodland		Lichen woodland
	42–43	
Main boreal forest		Closed-crown forest

Source: Hare (1950). Reproduced with the permission of the American Geographical Society.

In this respect, the 10 °C isotherm of the warmest month of the year has been considered coincident with the treeline for many years. Although this line parallels the position of the treeline across northern Canada, it generally lies further north, especially in continental areas (Tuhkanen 1980). Nordenskjöld's line (Nordenskjöld & Mecking 1928, p. 73) integrates the temperature of the warmest (v) and coldest (k) month of the year to define a polar line situated where $v = g - 0.1k$. Nordenskjöld was not clearly affirmative in relating this line to the treeline, as some ecologists have done since (Larsen 1974; Tuhkanen 1980). Nevertheless, it has been shown that this line represents an improvement in fit compared with the 10 °C isotherm (Larsen 1974).

Another approach uses the temperature sum over a given threshold as an isopleth value coinciding with the treeline position. The 3 °C isopleth (sum of positive monthly mean temperature/12) shows a good fit, although some departures exist locally between real and predicted positions of the treeline (Tuhkanen 1980). Similar results were obtained by Young (1971) using the 35 °C isopleth calculated as the sum of monthly positive means over 0 °C.

The precipitation component of climate was not considered by Hare (1950) to be a limiting growth factor for trees in eastern Canada. Hare suggested that a relation existed between the major north-eastern American vegetational zones and given values of Thornthwaite's potential evapotranspiration (Tab. 7.1). The circumhemispheric forest–tundra transition zone occurs where potential evapotranspiration is approximately 34–35 cm (Larsen 1980).

Bryson (1966) stressed the striking correlation between the northern forest border and the modal July position of the front that separates the Arctic air mass from the Pacific air mass in Canada. This correlation fits

Table 7.2. *Representative values of various thermal parameters*

	Western Canada (100°W–120°W)		Labrador-Ungava (60°W–80°W)	
	Treeline	Closed crown forest	Treeline	Closed crown forest
Net radiation (kly)				
annual	18	28	19	31
thaw season[a]	19	29	22	31
Thornthwaite's PE (cm)	34	43	28	41
Duration of thaw season (days)	120	168	145	175

Note: [a] Period with mean daily temperature >0 °C.

Source: Hare & Ritchie (1972). Reproduced with the permission of the American Geographical Society.

better west of Hudson Bay compared with the Labrador–Ungava peninsula, which is also influenced by a rather high frequency of 'United States' and Atlantic air masses. Preliminary results by Krebs & Barry (1970) suggested that the relation between the modal July position of the Arctic air mass and the northern vegetation boundary also holds over Eurasia. These authors point out that the position of the July Arctic air front is not *per se* causative of the vegetational boundaries but influences the local energy budget during the growing season. In this connection, Hare & Ritchie (1972) suggested that northern vegetational zonation coincides with given values of several radiation parameters. Mean total and absorbed solar radiation isolines drop sharply southward over Canada by as much as 20° between 150° and 70° west, as do northern vegetation boundaries. The mean yearly and seasonal net radiation values observed at the treeline and in the closed crown boreal forest are fairly stable over the area (Table 7.2). Values of 22 and 30 kilolangleys for the forest–tundra and taiga respectively have been reported from the Soviet Union (Skorupskii & Shelyag-Sosonko 1982). In Alaska, the 16 kilolangley isopleth matches the treeline better than either the 10 °C July isotherm or Nordenskjöld's line (Hare & Ritchie 1972). In comparison, the west–east discrepancy between the value of potential evapotranspiration and the duration of the thaw season indicates that these are less accurate indicators of the vegetational boundaries than the radiative parameters (Hare & Ritchie 1972).

A more reductionist approach, that is at the organism level, could shed some light on climate–vegetation relation in the boreal forest–tundra transition zone. Several valuable ecophysiological studies looking at tree physiology in cold environments have been carried out at the alpine

treeline, where low temperatures induce a negative carbon balance and hinder completion of the phenological cycle (reviewed by Tranquillini (1979)). In the Rockies, windy conditions during the winter are associated with high desiccation, abrasion and mortality in foliage of *Picea engelmanii* and *Abies lasiocarpa* which is unprotected by the snow pack (Hadley & Smith 1983, 1986, 1987). Winter water stress at the treeline should not be viewed as a universal phenomenon, however, since it has been suggested that *Abies balsamea* and *Picea mariana* do not experience it (Marchand & Chabot 1978). None the less, insufficient snow cover at the northern or alpine limit of several tree species results in stunted growth forms (Payette 1974) which are thought to have a higher photosynthetic to ligneous tissue ratio (Kulagin 1972).

In subarctic environments, the annual distribution of heat could be a more significant ecological factor than the mean annual temperature. For instance, it has been shown that white spruce growth is positively correlated with summer–fall temperature but inversely related to winter–spring temperature (Garfinkel & Brubaker 1980). However, work with black spruce at the treeline suggests that photosynthetic activity is more frequently limited by light intensity than by temperature during the growing season (Vowinckel, Oechel & Boll 1974). Some ecologists have argued that the problem of the treeline and the forest limit is one of population biology associated with the reproductive ecology of tree species (Marchand & Chabot 1978; Payette 1983). Black spruce seed viability (Elliot 1979*a*) and germinative capacity (Sirois 1988) appear to be related to the temperature gradient in the transition zone; experiments suggest that germination of this species is drastically reduced below 15 °C (Black & Bliss 1980). The threshold of 50% seed maturation in Scots pine requires 890 annual degree-days >5 °C, which is achieved at the treeline in only 2% of years (Henttonen *et al.* 1986). Because the minimum temperature sum for the development of a substantial number of flowering buds is approximately the same (Pohtila 1980), good seed-years occur very rarely in northern boreal and subarctic areas and a seed shortage is likely to occur at any given time.

In summary, one can find a certain degree of agreement between northern vegetation boundaries and many climatic indicators. However, none of them can yet be attributed with unequivocal causative significance (Carter & Prince 1981) because of insufficient ecophysiological knowledge about the major tree species. Nevertheless, at the formation level, thermic parameters such as radiative input and potential evapotranspiration show a global, but inaccurate, fit with major northern vegetational zones and give clues as to the nature of mechanisms operating at the limits. Moreover, the identification of a correspondence between the major boundaries and the modal position of the Arctic air

front in summer and winter may constitute a first step towards the interpretation of historical movement of the treeline and other boundaries in terms of Holocene atmospheric circulation patterns. To develop this, further improvement of the existing general circulation models, along with increased knowledge of the physiology and reproductive biology of northern tree species, is needed.

Spatiotemporal patterns in the boreal forest–tundra transition zone

Vegetation patterning in the transition zone landscape is linked to the low resilience of forest communities to disturbances. Intensive logging has resulted in anthropogenic tundra expansion south of the treeline in the Soviet Union (Tikhomirov 1961; Tyrtikov 1978). Reindeer grazing of tree seedlings (Hustich 1966) and catastrophic herbivore insect outbreaks (Kallio & Lehtonen 1973; Sepälä & Rasta 1980; Lehtonen 1977) have also induced fragmentation of the forest in the transition zone of Fennoscandia. Decreased flooding frequency in recent decades is associated with a low rate of regeneration in white spruce and current shifts from forest to tundra communities near the treeline in the Mackenzie area (Pearce, McLennan & Cordes 1988). However, none of these factors has the global effect of climatic change and climate-fire interaction in determining the pattern of the forested landscape in the transition zone. Consequently, it is these two processes which will be focused on in the following discussion.

The climatic change during the Holocene (Lamb 1977) is thought to be the main forcing factor in expansion and recession of northernmost forests in the Soviet Union (Tikhomirov 1961, 1963; Bray 1971; Khotinskiy 1984), in Fennoscandia (Hustich 1958; Karlén 1976, 1983; Kullman 1983, 1985) and in North America (reviewed by Ritchie (1984, 1987*a*)). Climatic changes having an astronomical origin induce a global influence on the biosphere. The Milankovitch theory (Berger *et al.* 1984), based on the earth's axial tilt and orbital eccentricity and the timing of the perihelion, predicts the general climatic trend during the past 18 000 years as shown in Fig. 7.3. The seasonality of the climate increased sharply during the Holocene between 16 000 and 6000 BP, with a maximum amplitude around 9000 BP corresponding to a summer and winter radiation difference compared with present values of +8% and −8% respectively (Kutzbach & Guetter 1986). Between 16 000 and 9000 years BP, the estimated July temperature was 2.5 °C higher than at present. Winter and summer precipitation was lower than at present between 15 000 and 12 000 years BP. From 9000 BP to the present, solar radiation has decreased over the Northern hemisphere (Ritchie 1987*a*). The

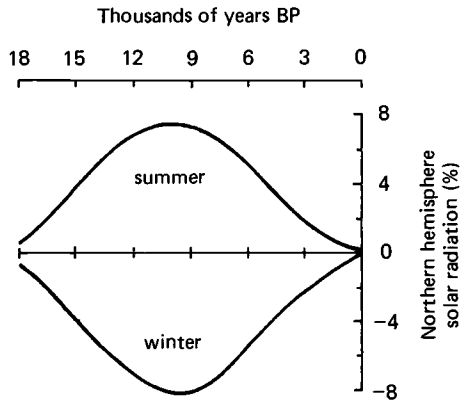

Fig. 7.3. Solar radiation departure from the present value in summer and in winter for the Northern hemisphere during the past 18 000 years according to the Milankovitch theory of climatic change. (Adapted from Kutzback & Guetter (1986); redrawn with the permission of the authors and the American Meteorological Society.

northern vegetation has reacted to the Holocene and recent climatic changes in various ways and with different lag periods, depending on the region.

Soviet Union

Holocene pollen and macrofossil records from the present taiga zone of the Soviet Union indicate afforestation beginning as early as 12 000 BP with arborescent birches and spruces. A general northward movement of the treeline between 8100 and 9200 BP is supported by several macrofossil trees found 100–200 km into the present tundra zone. These macrofossils consist of birches in western and eastern Siberia and of larches in the central Tamyr peninsula. Subsequent global cooling after 8000 BP resulted in a marked southward shift of the forest and transformation of northern taiga into forest–tundra in the western part of the country.

Another phase of forest progression occurred during the second half of the Atlantic period (6000–4600 BP). Spruce stumps from this epoch suggest that the tundra zone disappeared almost completely in the northern European USSR. Larch stump macrofossils substantiate forest encroachment 300, 100 and some tens of kilometers north of the present forest limit in the Yamal and Tamyr peninsulas and in the eastern maritime region respectively. Pollen and macrofossil evidence suggests a northern forest recession between 4600 and 4100 BP, a new advance between 4100 and 3200 BP and a degradation between 3200 and 2500 BP (Khotinskiy 1984). There are no literature reports of the response of

forests to the Little Ice Age in the Soviet Union. The last forest retreat left only scattered groves, witness to the past warmer climate, in the most sheltered sites of the modern tundra (Khotinskiy 1984). Northern forest vegetation of the Soviet Union has responded positively to the global twentieth century warming trend documented by Jones, Wigley & Kelly (1982) and Jones, Wigley & Wright (1986). Northward migratorial trends have been observed in tree species, and forests are now found on patterned ground generated under a former tundra environment (Tikhomirov 1961, 1963). In places, the movement of forest onto previously treeless areas is reported to be as rapid as 700 m per year (Uspenskii 1963, *in* Bray 1971).

Fennoscandia

The high elevation of northern Fennoscandia has meant that forest limit movements associated with Holocene climatic change have occurred along both altitudinal and latitudinal gradients. Karlén (1976, 1983) and Kullman (1987*a*) showed that Scots pine forests grew above the present limit of coniferous forests during the whole interval between 8000 and 3000 BP, even when the post-glacial isostatic rebound of 120–160 m is deducted. Although the exact timing of tree establishment is uncertain, the numerous Scots pine subfossils found up to 70 km north of its present limit testify to the presence of pine populations and therefore more suitable growth conditions sometime between 6000 and 4000 BP (Eronen 1979; Eronen & Hyvärinen 1982). Pronounced cold periods marked by glacier expansions and a lowered treeline occurred between 7500 and 7300 BP and around 4500, 2800 and 2200 BP, as well as in the recent Little Ice Age (Karlén 1976) when the estimated summer temperature was 2 °C lower than the modern average (Kullman 1987*b*). Downward movement of the pine forest limit in the Fennoscandian highlands was not a regular process during the post-hypsithermal period, since ^{14}C datings of dead logs found above the present forest limit cluster around 6800, 6000, 4600, 1500 and 900 BP, which are thus interpreted as warm periods (Karlén 1983). However, Kullman (1987*a*) pointed out the possibility of interpreting wood remains from certain periods as indicating either a climate warm enough to allow tree growth or a climate suitable for dead wood production and its long-term preservation. The Little Ice Age period was marked by a large-scale pine forest decline associated with a pronounced regeneration gap and increased mortality among mature individuals in the highlands of Fennoscandia (Kullman 1987*b*,*c*). There is no evidence that the pine forest limit has moved upwards during the relatively warm twentieth century (Karlén 1976), although numerous single trees germinated up to 150 m above the forest limit during the 1920s and 1930s (Hustich 1958). It thus seems that only exceptionally warm climatic

periods of relatively long duration (50–100 years) have been responsible for pine forest limit progression (Karlén 1976). In contrast, birch (*Betula pubescens*) in the northernmost part of Sweden has reacted strongly to the recent climatic change (Sonesson & Hoogesteger 1983). It has expanded upwards by up to 50 m and increased markedly in population density at lower altitude in response to the twentieth century 0.5 °C rise in temperature and 13% increase in precipitation.

North America

Despite the relative geographical uniformity of that part of northern North America east of Alaska, marked west–east differences in deglaciation chronology and post-glacial vegetation history exist (Ritchie 1987*b*). In the Mackenzie Delta, melting of glacial ice was completed by 15 000 BP and spruces succeeded shrub tundra around 10 000–9000 BP. Thus afforestation in most of western Canada occurred in the context of a hypsithermal climate, although most pollen data suggest that the vegetation response to the warmest period actually occurred somewhat later (Ritchie, Cwynar & Spear 1983). In contrast, the last remnant of Laurentide ice sheet persisted until approximately 6500 years BP on the central Quebec–Labrador peninsula (Vincent 1989). Spruce migrated rapidly into this area (Richard 1979, 1981*a*; Richard, Larouche & Bouchard 1982) under deteriorating climatic conditions (Lamb 1985; Ritchie 1987*b*).

Paleodata from the forest–tundra transition zone of the Northwest Territories consistently suggest that earlier during the Holocene, forests either occupied positions north of the present forest limit or were more continuous into the transition zone than at present. On the Tuktoyaktuk peninsula (Northwest Territories), the following vegetation sequence has been suggested (Ritchie & Hare 1971):

12 900 to 11 600 years BP	dwarf birch tundra
11 600 to 8500	forest–tundra
8500 to 5500	closed-crown spruce–birch forest
5500 to 4000	tall shrub tundra
4000 to present	dwarf birch heath tundra.

The authors suggested that the shift from forest to tundra was associated with a southward displacement of the modal July position of the Arctic air front of 350 km compared with its location during the hypsithermal period. Other works in the same area, using pollen and macrofossil analysis, support the hypothesis of a retreat of the continuous forest limit during the second half of the Holocene period (Hyvärinen & Ritchie 1975), possibly 50–70 km south of its maximum extension (Spear 1983). Nichols (1974, p. 652) argues that several fluctuations of the continuous

forest limit occurred in central Canada during the whole post-glacial period, with a maximum extension of approximately 250 km north of its present position between 5500 and 3500 BP. However, because no fossil logs have been found, the former presence of forests in this area remains to be proved (Payette & Gagnon 1979, 1985). East of Hudson Bay, early Holocene landscape vegetational dynamics associated with climatic changes have mostly been documented south of the treeline. Periods during the early Holocene in which spruce pollen was relatively more abundant than now can be bounded between 4200 and 3200 BP in the James Bay area (Richard 1979), 5200 and 4700 BP in central northern Quebec (Richard, Larouche & Bouchard 1982) and 4700 and 3500 BP in Labrador (Lamb 1985). The subsequent decrease in relative abundance of spruce pollen is clearly interpreted by Lamb (1985) as a signal of a reduction of forest cover in the forest–tundra transition zone following deteriorating climate and fire–climate interaction.

During the Little Ice Age, the early explorer Samuel Hearne drew a map suggesting that the treeline in the Keewatin district, west of Hudson Bay, was further south and west of its present position by up to 100 km (Ball 1986). The situation seems to have been quite different east of Hudson Bay where data suggest that the treeline moved only a short distance in response to the Little Ice Age climate (Payette & Gagnon 1979; Gagnon & Payette 1981). On the Quebec–Labrador peninsula, black spruce went some tens of kilometers north of the present treeline and the species limit is thought to represent the remnant of the forest limit during a warmer episode (Payette & Gagnon 1979), the dating of which is currently under investigation. As in Fennoscandia and the Soviet Union, the global warming trend of the twentieth century has induced local treeline expansion or increased seedling establishment near the forest limit in Alaska (Griggs 1937), in central Canada (Scott, Hansell & Fayle 1987) and in northern Quebec (Morin & Payette 1984; Payette & Filion 1985).

This review has illustrated the sensitivity of the northern forest border ecosystem to climatic change. A certain degree of circumhemispheric synchronicity can be observed in the vegetation response during the early post-glacial hypsithermal, and during the twentieth century warming (Fig. 7.4). Corresponding global northern forest retreat seems more difficult to warrant for lack of macrofossil evidence. Some climatic changes could be associated with the distribution of the total amount of heat received by the earth and have only a regional effect on the vegetational landscape. Predicted higher sensitivity to climatic warming of coniferous forests in maritime areas (Kauppi & Posch 1985) could also account for inter-regional differences in vegetation response. However, the data presently available are still too diffuse to corroborate this

Fig. 7.4. Schematic representation of selected reports of tree population fluctuations in response to Holocene climatic forcing in the circumhemispheric boreal forest–tundra transition zone. Shaded section of the rectangles represents a time-coincident event; bold bars represent single data points. Upper scale represents forest progression; lower scale, forest regression.

possibility. On the other hand, several pointers suggest that disturbances, and forest fires in particular, could act in a synergic way with the climate to influence the vegetational landscape dynamics in the forest–tundra.

The role of fire in the holocene development of the boreal forest–tundra transition zone

Wildfires have been recognized as a driving ecological factor in boreal coniferous forests of the Soviet Union (Barney & Stocks 1983; Antonovski, Ter-Mikaelian & Furyaev, Chapter 14 of this volume), in northern Fennoscandia (Zackrisson 1977) and in North America (Heinselman 1981*a*). They play a major role in releasing nutrients locked up in dead and living organic matter (Van Cleve & Viereck 1981) and prescribe the start and end of vegetational successions (Dix & Swan 1971; Maikawa & Kershaw 1976; Black & Bliss 1978; Foster 1985; Morneau & Payette 1989). Wildfires control the age structure of forest stands (Van Wagner 1978; Cogbill 1985; Johnson & Van Wagner 1985; Sirois & Payette 1989), influence species composition and physiognomy of the vegetation (Johnson & Rowe 1977), and are a determinant of diversity and stability throughout the vegetational landscape (Heinselman 1981*a*; Romme 1982; Baker 1989). In steady-state conditions, fires act as a natural disturbing agent, triggering numerous mechanisms that lead to forest community renewal.

In areas where climate has limiting effects on tree growth and development, numerous examples suggest that wildfires could have a much more

drastic effect on the vegetation landscape development. Several pronounced fire-induced depletions of tree populations and shifts from forest to tundra communities have been reported in the transition zone of various regions including northern Sweden (Zackrisson 1977), Siberia (Kriuchkov (1968*a*,*b*) quoted by Wein (1975)) and northern North America (Hustich 1951*a*, 1966; Lutz 1956*a*; Ritchie 1962). It is suggested that this phenomenon, recurring over a long period of time, could have shaped the modern configuration of the forest–tundra.

Radiocarbon dating of charcoal found at the podsol surface of some treeless sites in the forest–tundra transition zone of Keewatin (Bryson, Irving & Larsen 1965) testifies to a 280 km fire-induced deforestation south of the modern treeline some 3500 years ago. Payette & Gagnon (1985) suggest that the modern forest–tundra of north-eastern North America is the end-product of a once densely populated coniferous zone that experienced long-term deforestation during the Holocene period. They provide datation of conifer charcoal from 116 predominantly treeless sites along a south–north transect in the forest–tundra east of Hudson Bay. The results show that a fire-induced deforestation process has been active in this area during the past 3000 years, particularly between 3000 and 2100 BP, 1800 and 1050 BP, 800 and 650 BP and 450 and 100 BP. The latitudinal position and age of the sampled charcoal suggests that there is no relation between the onset of deforestation and the distance from the present treeline. Intensive charcoal sampling in a much smaller region revealed fire-induced deforestation periods from 2350 to 2100 BP, 1650 to 1450 BP, 1350 to 1050 BP, 850 to 650 BP and 400 to 200 BP (Millet & Payette 1987). These periods fit well with those found over a large area by Payette & Gagnon (1985) and match to a considerable extent the cold climatic periods identified on the basis of sand dune development in the same general area (Filion 1984). Instead of a large-scale southward movement of the forest–tundra zone and treeline as reported in Keewatin (Bryson, Irving & Larsen 1965; Nichols 1974, 1975), the data provided by Payette and his associates suggest a progressive fragmentation of the forest cover in the forest–tundra transition zone during the past millennia. Deforestation did not occur at each fire event; periods of successful post-fire forest recovery have been identified between 3500 and 2700 BP, 2000 and 1600 BP (Gagnon & Payette 1981) and between 2100 and 1800 BP, 1050 and 800 BP and 650 and 450 BP (Payette & Gagnon 1985). Post-fire regeneration success hinges mainly on the regenerative potential of the tree species and on the coincidence of a fire and a climatic period more or less favorable to tree reproduction.

The effect of the climatic cooling trend of the Holocene on post-fire forest regeneration capacity can be assessed by the evaluation of fire impact on tree populations distributed along a south–north climatic

Table 7.3. *Percentage of upland (U) and lowland (L) sites in each post-fire density:pre-fire density ratio class*

	BF[a]		FFTs		FFTn		SFT	
Ratio class	U	L	U	L	U	L	U	L
0.00—0.25	21.6	7.8	45.8	25.0	44.0	8.0	92.9	12.5
0.26—0.50	15.7	7.8	20.8	37.5	16.0	6.0	5.4	19.6
0.51—1.00	15.7	11.8	16.7	25.0	18.0	16.0	0.0	16.1
1.01—2.00	21.6	35.3	12.5	10.4	18.0	38.0	0.0	30.4
>2.00	25.5	37.3	4.2	2.1	4.0	32.0	1.8	21.4

Note: [a] BF: upper boreal forest; FFTs: southern part of the forest subzone; FFTn: northern part of the forest subzone; SFT: shrub subzone.

gradient. The large fires of the 1950s, which burned over 5500 km^2 of land vegetation in representative parts of the upper boreal forest and the forest–tundra of northern Quebec, provide an opportunity to address the question of the role of fire in the Holocene development of forest–tundra at the demographic level. Black spruce forms almost monospecific forests in that area. Since seedling establishment of black spruce is very low after 20–25 post-fire years, owing to seed shortage (Morneau & Payette 1989; Sirois & Payette 1989) and increase in lichen cover (Brown & Mikola 1974; Cowles 1982), stand density appears to be determined by the relative success of seedling establishment during the early stage of stand development. Sirois & Payette (1991) evaluated tree population density immediately before and 30 years after 1950s fires in 410 sites in northern Quebec representative of four eco-regions distributed along a south–north climatic gradient. They found that low post-fire regeneration occurred in the uplands whereas the regeneration was high in the sheltered and more humid lowlands (Table 7.3). The long-term maintenance of closed-crown forest appears to be associated with a high seedling density in the initial stage of post-fire forest recovery. The impact of fire on tree population density in the uplands was most pronounced in the shrub subzone of the forest–tundra, where 93% of the krummholz stands experienced a minimum drop in population density of 75%. A pronounced decrease in population density was recorded in nearly half of the upland arborescent populations of the forest–tundra. Successive depletion of the tree population following several destructive fires appears to be the main deforestation process in the southern forest–tundra, whereas krummholz stands of the northern forest–tundra are frequently removed by a single fire event. More than one fifth of the upland samples from the upper boreal forest, where post-fire regeneration is generally successful, showed a minimum drop in tree population density of 75%.

Paleofire records (Desponts 1990) and the fire rotation period for the upper boreal forest (Payette *et al.* 1989*b*) suggests that 70 fire cycles have occurred in this area since it has been afforested (Sirois & Payette 1991). If each of those fires had had the same effect as the 1950s fires, then the boundary between the boreal forest and forest–tundra would be far south of its present position. The marked decrease in the tree density of a significant proportion of the northern boreal forest upland sites could be considered as an important step toward the southward expansion of the forest–tundra, several tens of kilometers into the boreal forest. This would suggest that the 1950s fires were particularly destructive. The fires occurred at a juncture between fifty years of a global warming trend, during which the fuel built up, and a cooling trend in the subsequent decade (Jones, Wigley & Kelly 1982; Jones, Wigley & Wright 1986) potentially hindering post-fire regeneration. The overall deforesting effect of the 1950s fires suggests that short-term (*c.* 10 years) climatic fluctuations could be of high biogeographical significance for long-term vegetation dynamics in the transition zone. Since low viable seed production at the treeline seems a general rule (Elliot 1979*a*; Black & Bliss 1980), it would appear justifiable to assume that cold climatic conditions in the forest–tundra are more limitative to tree sexual reproduction than to tree growth. With regard to the long-term maintenance capacity of black spruce populations in fire-free conditions near the treeline (Payette *et al.* 1985, 1989*a*), it is suggested that the present patchy vegetation pattern of the north-eastern north American forest–tundra is associated with catastrophic fires during climatic periods of the Holocene that were detrimental to tree reproduction (Fig. 7.5). Tree reproductive biology appears as a keystone of the forest–tundra ecology in this area. The global validation of this hypothesis requires further knowledge of fire ecology and reproductive characteristics of the tree species in the Fennoscandian and Siberian forest–tundra.

Concluding comment

Many important dimensions relating to the forest–tundra vegetational pattern have not been addressed in this chapter. These include, for example, permafrost distribution, nutrient cycling, light characteristics, moisture gradients and plant communities. Interested readers are referred to Van Cleve *et al.* (1986), Larsen (1989) and Bonan & Shugart (1989) for excellent treatment of these topics.

Despite regional variations due to species composition, the boreal forest–tundra transition zones of North America, Fennoscandia and the Soviet Union display some structural analogies in latitudinal zonation. This circumhemispheric belt has been characterized by instability at the

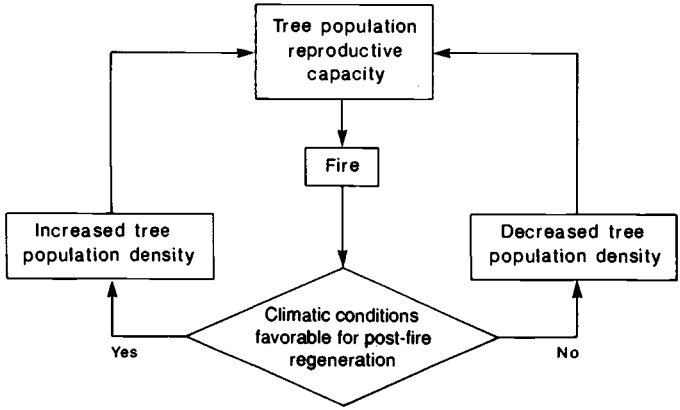

Fig. 7.5. Hypothetical effect of the fire–climate interaction on high-latitude forests. Other factors being equal, post-fire regenerative capacity is related to pre-fire stand density. Recurrent fires during climatic periods conducive to high reproductive capacity maintain a closed-crown canopy, as is the case in boreal forest. Recurrent fires when the climate is limitative to seed production and seedling establishment result in open woodlands and barelands. Post-fire seedbed conditions are very variable over short distances and have a considerable influence on tree reproduction success. This is why fire impact on subarctic tree density at the landscape level is highly variable.

community and landscape levels during the past millennia and appears especially responsive to climatic change as exemplified by several instances of progression or recession of forest populations reported in this chapter. In the context of a significant warming trend, current forest succession models predict pronounced qualitative community changes in the southern boreal forest which will bring it closer, in floristic terms, to the higher diversity, northern deciduous forest (Solomon 1986; Pastor & Post 1988). However, most of the productivity increase is expected to occur in the transition zone, where large expanses comprising low-density populations and bare ground previously covered by forest are available for afforestation. Community inertia and a lag response to the climatic warming trend (Davis & Botkin 1985; Solomon 1986; Payette *et al.* 1989*a*) might, however, slow the pace of this progression. Simulation and field studies are currently under way to investigate whether forest fires can act as a catalyst to increase the rate of vegetational change induced by the climatic trends in the boreal forest-tundra transition zone. I hypothesize that open lichen woodland subjected to recurrent fire offers one of the most promising opportunities to predict the mean and long-term effects of the global warming trend on the boreal zone.